

COMPOSITION, INVASIBILITY, AND DIVERSITY IN COASTAL CALIFORNIA GRASSLANDS

MARK R. STROMBERG

Hastings Natural History Reservation, 38601 E. Carmel Valley Road,
Carmel Valley, CA 93924-9141, Museum of Vertebrate Zoology,
University of California, Berkeley, and Natural Reserve System,
University of California

PAUL KEPHART

Rana Creek Habitat Restoration, 35351 E. Carmel Valley Rd.,
Carmel Valley, CA 93924-9141

VERN YADON

Director Emeritus, Pacific Grove Museum of Natural History, 1119 Buena Vista,
Pacific Grove, CA 93950

ABSTRACT

We present a detailed floristic study of coastal terrace prairies in central California that are poorly described in California's ecological literature. Definitive native grasses include *Danthonia californica* Bolander, *Nassella pulchra* (A. Hitchc.) Barkworth, and *Festuca rubra* L. Definitive native forbs include *Baccharis pilularis* DC., *Viola*, *Sidalcea*, *Cammissonia*, and *Acaena*. Species richness in the coastal prairies (1 m²) averaged 22.6, nearly twice that of relatively diverse serpentine California grasslands, and other North American grasslands. We sampled 33 coastal prairies and found 340 plant species including 258 forbs. Nearby plant communities (Monterey Pine, Coastal Scrub) had much lower species diversity at all spatial scales studied. Three distinct coastal grasslands, each associated with a land form, can be defined by distinct species composition; coastal terraces, uplifted "bald hills," and inland ridges. We compared 29 coastal terrace prairies (those without tree or shrubs) to 80 inland *Nassella* prairies with regard to 27 floristic variables (cover, number of natives/exotics, perennials/annuals, grasses/forbs) along a gradient from interior-coastal valley and from north to south along the coast. Coastal terrace prairies were invaded by exotics, but far less so than inland *Nassella* prairies. Species diversity (0.1 ha) and total cover were positively correlated. Relative cover of exotic species was negatively correlated with total cover, based on all sites. Number of exotic species was positively correlated with species richness in inland *Nassella* prairies but not in coastal terrace prairies. Canonical correspondence analysis indicated that coastal terrace prairies with higher cover of non-native species had reduced total cover and/or reduced diversity of native perennial species of grasses and forbs. Native perennial grasslands, including coastal terrace prairies, are rare and have been eliminated by development along the narrow corridor of land between the sea and the inland ridges of central, coastal California. If protection of biodiversity is a management goal in land use plans, coastal grasslands should be protected as biodiversity "hotspots".

INTRODUCTION

Native perennial grasslands in California are among the most endangered ecosystems in the United States (Peters and Noss 1995). An area of approximately 7,000,000 ha (about 25% of the area of California) formerly in native grassland or foothill savanna, is now dominated by exotic grass species primarily of Mediterranean origin (Huenneke 1989). Typical annual grassland species include *Bromus diandrus* Roth, *B. mollis*, *B. rubens* L., *Avena barbata* Link, *A. fatua* L., *Erodium cicutarium* (L.) L'Hér., *E. botrys* (Cav.) Bertol, and *Vulpia myuros* (L.) C. Gmelin (Heady et al. 1988). Conversion to exotic annual vegetation was so fast, extensive, and complete that the original extent and species composition of most native perennial grasslands is unknown (Burcham 1957; Barry 1972; Keeley 1989; Heady et al. 1992; Holland and Keil

1995). Cover of exotics is often over 80% in this annual grassland vegetation type (Biswell 1956). Yet, small, isolated stands of native perennial grasslands still occur and these stands have been used to define "valley grassland" (White 1966b, 1967; Robinson 1971), presumably once dominated by *Nassella* (Heady et al. 1988). Extensive fragmentation of relict grasslands continues (Barry 1972) and even within protected natural areas (Hastings, San Bruno Mountain, Jepson Prairie, Santa Rosa Plateau), relatively "pure" stands of native grasses occur in smaller, interior patches. Few studies have been published to describe the original grassland composition or that of presumed remnants. The widely held view that interior annual grasslands of California were originally dominated by perennial grasses (primarily *Nassella*) is based on limited evidence (Hamilton 1998). The view that succession proceeds in these interior grasslands to dominance

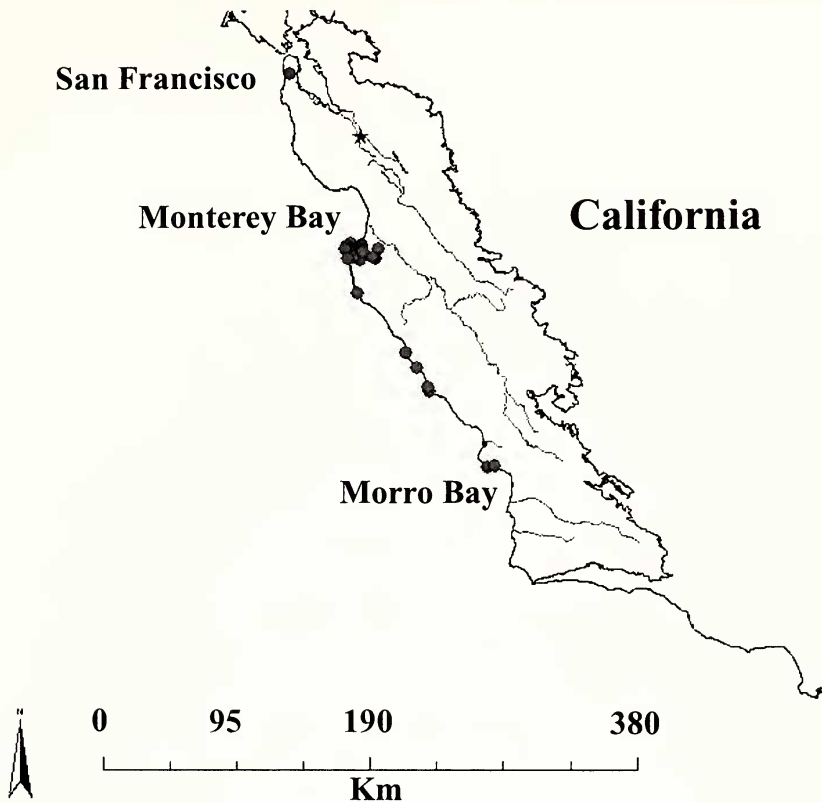


FIG. 1. Map of study sites on coastal California.

by *Nassella* (Heady et al. 1988) is not supported by long-term studies (Stromberg and Griffin 1996) or a critical review of evidence (Hamilton 1998). Large areas of the interior "valley grassland" (Heady et al. 1988) may have been dominated by native, annual forbs (Schiffman 1994; Schiffman 2000). Identification of these rare, scattered patches of high biodiversity continues to be a critical activity for conservation (Myers et al. 2000). GAP analysis and remote sensing serve as useful tools, but to identify the most important habitats at a finer geographic scale, we need intensive field surveys using classical methods, as presented here.

The purpose of this study is to demonstrate that California's coastal grasslands are previously unrecognized biodiversity hotspots. We will do this by presenting patterns of diversity, describing major gradients in diversity within habitats and compare the coastal grasslands with other nearby habitats and other United States grasslands.

California's coastal grasslands are poorly described in the literature. "Coastal terrace prairie" has had widely varying interpretations. (Kuchler 1964) described "coastal grasslands" in a general way. Others have defined "north coast prairies" by listing dominant species that extend from the Mendocino coast south to Point Lobos (Heady et al. 1988). They described north coast prairies as being dominated by *Festuca idahoensis* Elmer, *F. rubra*

and *Danthonia californica*; they used the term "coastal terrace prairie" to describe this community. "Northern coastal grassland community" with the same dominant grasses, as well as *Calamagrostis nutkaensis* (C. Presl) Steudel and *Deschampsia cespitosa* (L.) Beauv., has been described as extending from San Francisco northward to the Klamath Mountains and in patches south to San Luis Obispo (Holland and Keil 1995). Finally, a "tufted hairgrass community" has been defined where *Danthonia* is dominant—this series is part of the "coastal prairie, which extends inland from terraces to bald hills" (Sawyer and Keeler-Wolf 1995). Such "bald hills" are a common feature along the coast and arise abruptly inland from the coastal terraces. Coastal prairies occur on poorly drained soils, often clays derived from serpentine outcrops, and often occur on a series of former coastal terraces that through geological action have been moved inland and uplifted. As one moves inland, "ecological staircases" grade into drier, higher interior ridges (Westman 1975; Cylinder 1995). Most of these interior ridges are forested, but many sustain open grasslands. Further inland, conifer forests are replaced by oaks and typical "annual grassland" oak savanna (Barbour and Major 1995, Holland and Keil 1995). Monterey pine forests are often adjacent to coastal terrace prairies in the central coast of California. Shrubs (e.g., *Baccharis*)

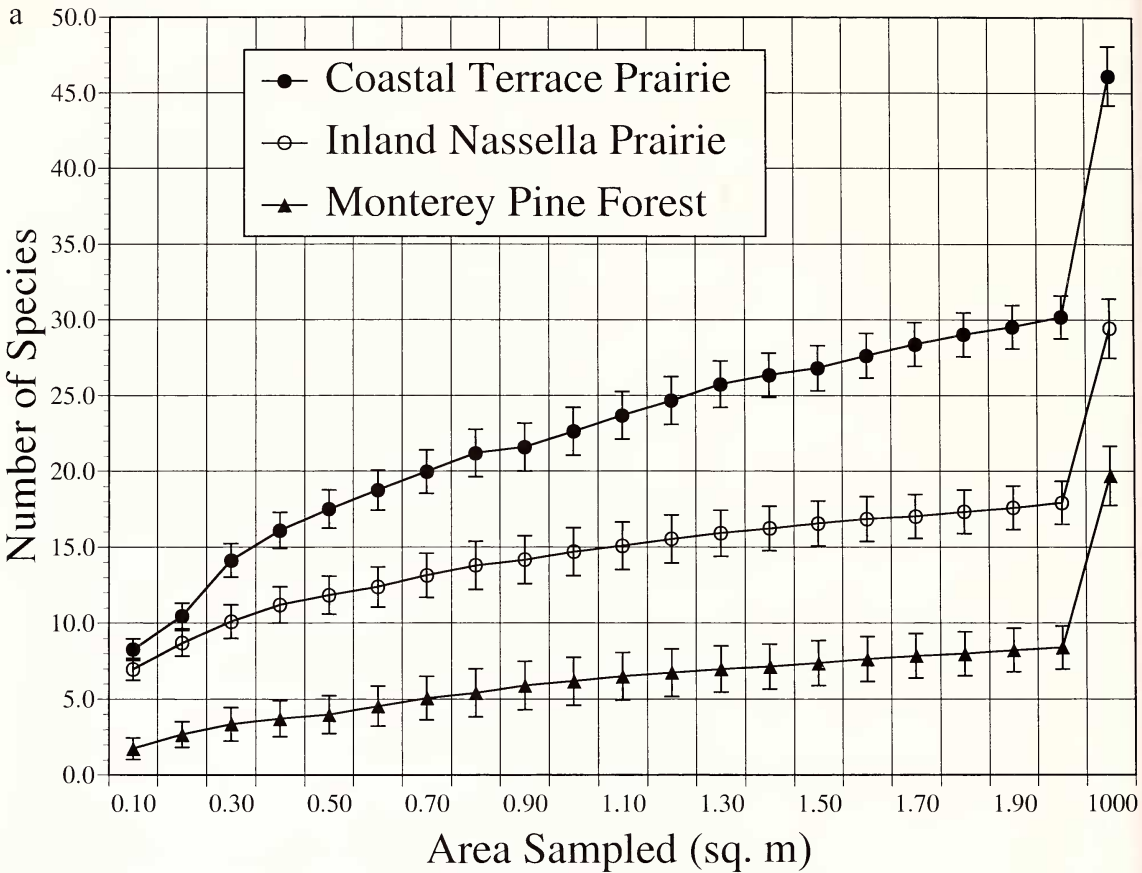


FIG. 2. a) Average number of species present as sampling areas are added in three coastal California plant communities, ± 1 standard error.

(McBride and Heady 1968) or trees (e.g., *Pinus radiata* D. Don) (Callaway and Davis 1993) invade these coastal grasslands without fire or grazing. Pre-settlement fires in coastal grasslands were frequent, with 2–10 year return intervals (Greenlee and Langenheim 1990). Post-settlement disturbances have included year-round grazing by domestic livestock (Mack 1989). In most descriptions of coastal grasslands, *Nassella pulchra* is a co-dominant.

Native perennial grasslands persist along a continuum ranging from dominance by non-native species to being relatively free from exotics (Harrison et al. 2001). In this case, we examined species composition, invasibility, and diversity change along a gradient from central coast terraces inland to California's central coastal mountain ranges (here, the Sierra de Salinas). Our previous studies of the inland *Nassella* prairies investigated the role of gophers, grazing, and historic cultivation (Stromberg and Griffin 1996). Here, we extend our studies towards the coast to include grasslands that can be recognized as coastal terrace prairies by the constant presence of *Danthonia californica* and *Nassella*. We provide a background of data on the more

general discussion of patterns in species diversity (Tilman et al. 1997, Huston et al. 2000, Kaiser 2000) and the relationship between species diversity and invasive species (Symstad 2000) in landscape studies (Stohlgren et al. 1997).

STUDY AREAS

Thirty-three stands of coastal terrace prairie were sampled, from Avila Beach, north along the Big Sur coast to Pebble Beach and then north from Santa Cruz to San Bruno Mountain near San Francisco (Fig. 1). Stands were selected based on previous extensive botanical surveys of central coastal California grasslands (Kephart 1993; Yadon 1995; Stromberg and Griffin 1996). Stands were not recently grazed or cultivated and were initially selected based on co-dominance of *Deschampsia* or *Danthonia*.

Data from other studies were discovered and used. In 1965 and 1966, 46 homogenous stands of Monterey pine (*Pinus radiata*) forests were sampled from Cambria to Año Nuevo (White 1966a, Vogl et al. 1988). In 1993, 141 homogenous stands of coastal scrub were sampled from San Simeon to

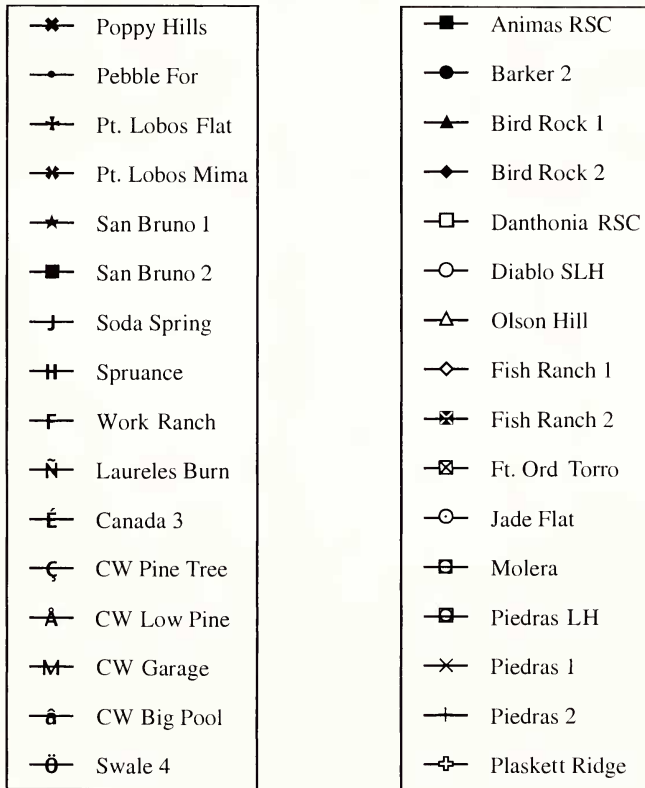
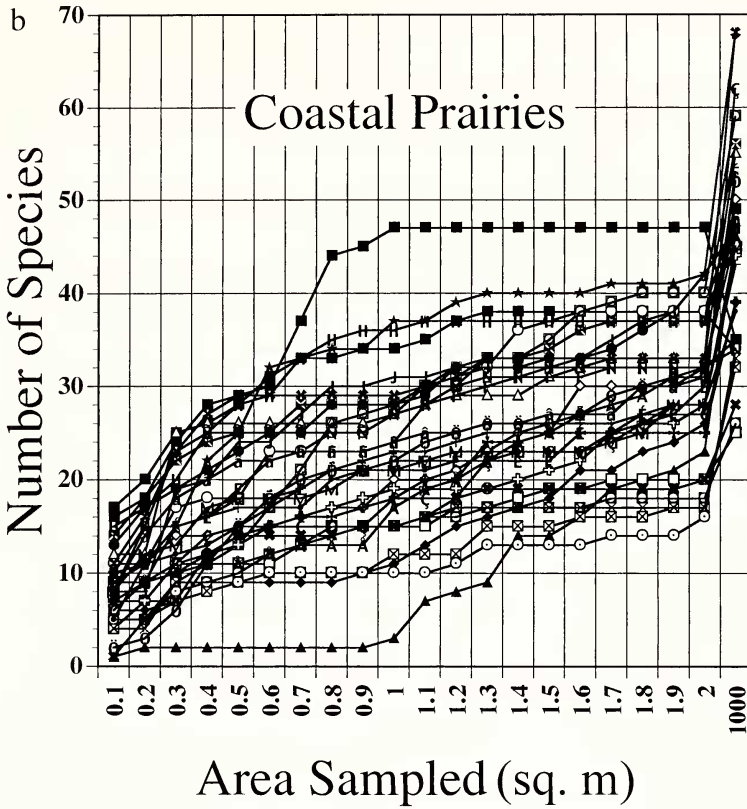


FIG. 2. Continued. b) Species/area curves for individual sampling localities.

Point Lobos (Heuer 1994). In 1991, 80 inland *Nassella* prairies in the Sierra de Salinas were sampled (Stromberg and Griffin 1996). Species richness depends on the scale of sampling (Gross et al. 2000) so comparisons to other studies were made at similar scales (1 sq. m).

METHODS

Sampling was done at the peak of the flowering season, from mid-April through May in 1996 and 1997. At each grassland stand (Fig. 1), we chose a homogenous area and flagged a 50 m × 20 m plot (0.1 ha) with the long axis parallel to topographic contours. We recorded presence of all plant species we could discover on the larger plots. Starting from the midpoint of the short axis, we placed steel quadrats (20 cm × 50 cm; 0.1 m²) at 2.5 m intervals along the 50 m midline of the 0.1 ha plot (20 quadrats/plot). For each quadrat, we recorded a cover class for canopy cover of all plant species we observed (Daubenmire 1959). Quadrats were painted to facilitate recognition of Daubenmire cover classes. A cover value of 0.01 was assigned to each species seen only in the larger plot and not seen in any smaller quadrat. Cover for each species at each stand (site) was calculated by averaging midpoints of the cover classes assigned to each of species in the 20 quadrats. Stands were at least 200 m apart, and more often, many kilometers apart. For each stand, we recorded aspect, elevation, distance inland from the coast, latitude and longitude (UTM), total number of plant species (Hickman 1993), soil type, land form, number of grasses and forbs, and numbers of perennials and annuals, native and exotic. Species were counted based on scores in successive quadrats on original field sheets; one coastal terrace data sheet was inadvertently lost after transcribing summary numbers so the species tally by area for one coastal terrace is missing. Nine soil series were included (Cook 1978; Ernstrom 1984). Land forms of coastal terrace prairies include: 1) coastal terraces immediately adjacent to the ocean that are almost level; 2) grasslands on the sides of isolated bald hills arising inland and up at least 10 m from the terraces, sometimes locally known as "potreros"; and 3) drier, inland ridges well over 100 m above the coastal terraces and bases of the inland mountain ranges. Staviw 5.0 (SAS) was used for statistical comparisons. Bonferroni/Dunn post-hoc tests were included to show individual differences in pairwise comparisons ($P = 0.05$). We used several methods to order stands based on species composition and with regard to measures of diversity, including CCA, DCA and Bray-Curtis ordinations (PC-ORD ver 4) (ter Braak 1987a, b; McCune and Mefford 1999). Stand coordinates in our ordination were based on species data. We dropped species that occurred in only one stand with a cover value less than 5% in order to reach a numerical solution for CCA. Computational prob-

lems (Tausch et al. 1995) have been addressed, and the method we used is inherently robust (Leps and Hadincova 1992).

Species composition of the herb layer was observed using similar methods in 46 stands of Monterey pine forests. Discovery of archival records (K. White, unpublished data, Hastings archives) allowed us to include observations from 40 to 80 quadrats (20 cm × 50 cm; 0.1 m²) that were read as above for plant cover. A larger area of 0.1–1 ha was then searched for additional species present and each was recorded (K. White, unpublished data; Hastings archives).

Discovery of additional comparable data allowed us to include comparisons to coastal shrub communities (Heuer 1994). Coastal shrub communities, often adjacent to coastal terrace prairies, were sampled with 16 sq. m quadrats at 141 locations, again at the peak of the flowering season, in 1993. No larger sampling areas were surveyed for additional species (Heuer 1994) and only the larger (16 sq. m) quadrats were used.

Inland *Nassella* prairies were described in detail previously (Stromberg and Griffin 1996). We included inland prairies in this study to examine the larger scale differences across the landscape as inland *Nassella* prairies share *Nassella* and other species with coastal terrace prairies, but occur at a drier, inland part of an environmental continuum occupied by native grasslands in coastal California. Data sets from this study will be made available (ESA Ecological Archives or NRS archives).

RESULTS

Average species richness varies with the area sampled (Fig. 2). For individual sites, most reach an asymptote by about 2 m (Fig. 2a). No definitive asymptote is reached for the average coastal terrace prairie/Monterey pine forest (CTP) or (MPF). Species counts at 0.1 ha represents the best estimates for total species richness. Mean species numbers between all pairs are significantly different (paired t-tests, $P < 0.001$) for comparisons at 1 sq. m. and at 0.1 ha (Table 1).

This comparison of species richness with area leads to an interesting observation on the effects of a major human-directed use of the ecosystem. In a previous analysis of inland *Nassella* prairie stands with and without active grazing by domestic cattle, significantly fewer plant species were observed in grazed stands (Stromberg and Griffin 1996) based on areas of 0.1 ha. In this analysis of species number at a smaller sampling scale (1 sq. m), this pattern in species richness was reversed and is clearly dependent on scale (Fig. 2).

Coastal grasslands have much greater species richness in comparison to inland *Nassella* grasslands, coastal pine, or coastal scrub plant communities. A total of 82 species of grasses or sedges and 258 species of forbs (340 total) were found in

TABLE 1. COMPARISONS OF SPECIES DIVERSITY BETWEEN COASTAL TERRACE PRAIRIES (CTP), INLAND *NASSELLA* PRAIRIES (INP) AND MONTEREY PINE FORESTS (MPF) BASED ON FIRST TEN 0.1 SQ. M OBSERVATIONS (1 SQ. M) IN EACH SAMPLE. Coastal scrub species density was derived from 16 sq. m. quadrats at each stand, expressed here as species/sq. meter using $S = cA^z$ where $z = 0.25$.

Number of species per square meter	Count	Mean	Std. err.	
Coastal Terrace Prairies	32	22.6	1.58	
Inland <i>Nassella</i> Prairies	80	14.7	0.78	
Monterey Pine Forests	46	6.2	0.58	
Coastal Scrub	141	5.5	0.20	
Comparison of means (INP, CTP, MPF)	DF	Mean square	F value	P-value
Category	2	2615.2	62.9	<0.0001
Residual	155	41.6		

33 coastal terrace prairie stands. In 80 inland *Nassella* prairie stands, a total of 194 species were found; 136 plant species were found in 48 coastal Monterey pine stands (Vogl et al. 1988). Many fewer plant species (65 total) were found in 141 coastal scrub stands. Species richness (species/sq. m) in coastal prairies is about 3.5 times greater than in adjacent Monterey pine forests (Table 1) and nearly 4 times greater than in adjacent coastal scrub. Coastal prairies also have a much greater species richness compared to other grasslands in California

and North America (Table 2) when each is presented at a comparable scale (1 sq. m).

Preliminary Bray-Curtis ordinations of the 33 stands revealed that both stands at Bird Rock and both forest stands in Pebble Beach (Poppy Hills, 24 Padre Lane-Table 4) were outliers. Although eliminated, they offer insights to dynamics of coastal prairies. Samples at Bird Rock had unusually high cover of *Carex pansa* L. Bailey (68% and 18%, respectively). *Carex pansa* was only found in two other stands, and there it was not abundant (cover

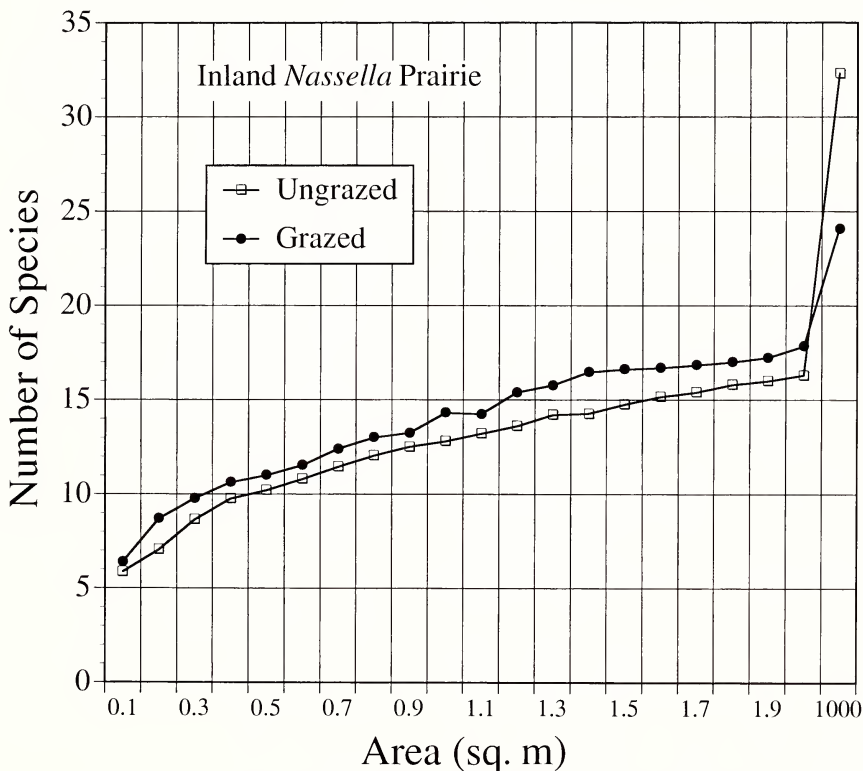


FIG. 3. Average number of species present as sampling areas are added in 43 ungrazed (1937–1991) inland *Nassella* prairies and 37 grazed (1880–1991) inland *Nassella* prairies (Stromberg and Griffin 1996).

TABLE 2. COMPARISON OF SPECIES RICHNESS (SPECIES/SQ. M, \pm SD OR \pm SE) IN CALIFORNIA GRASSLANDS AND OTHER ARID WESTERN PLANT COMMUNITIES. Species codes: Agr spi, *Agropyron spicatum*; Agr smi, *Agropyron smithii*; Amo can, *Amorpha canescens*; Art tri, *Artemesia tridentata*; Fes ida, *Festuca idahoensis* Elmer; Sti let, *Stipa lettermanii*; Poa pra, *Poa pratensis*.

Community name	Species density	Reference
Coastal Terrace Prairies	22.62, \pm 8.9	This study.
Napa Co.-L. Berryessa, CA Serpentine Meadows	12.3, \pm 2.3	(Harrison 1999)
Napa Co.-L. Berryessa, CA Non-Serpentine Meadows	10.3, \pm 2.2	(Harrison 1999)
Monterey Co., Sierra de Salinas, CA Annual Calif. Grassland	14.7, \pm 0.7	(Stromberg and Griffin 1996)
Bighorn Basin, C. WY Agr spi/Art tri	10.2, \pm 0.5	(Stohlgren et al. 1999a)
Grant Teton, NW WY Agr spi/Art tri	8.9, \pm 0.6	(Stohlgren et al. 1999a)
Gunnison, W. CO Sti let/Art tri	8.8, \pm 0.4	(Stohlgren et al. 1999a)
Wind Cave, W. SD Poa pra/Amo can	8.7, \pm 0.5	(Stohlgren et al. 1999a)
Charles Russell NWR, E. MT Agr smi/Art tri	4.6, \pm 0.5	(Stohlgren et al. 1999a)
Yellowstone, W. WY Fes ida/Art tri	9.0, \pm 0.6	(Stohlgren et al. 1999a)
Pipestone N.M., S. MN Tallgrass Prairie	12.2, \pm 0.7	(Stohlgren et al. 1999b)
Cheyenne, SE. WY Mixed-grass Prairie	10.7, \pm 0.5	(Stohlgren et al. 1999b)
Pawnee Butte, NE CO Short-grass Prairie	8.5, \pm 0.4	(Stohlgren et al. 1999b)

<5%). Bird Rock 2 was the only stand to have more than 10% *Lolium multiflorum* Lam. with 34.4%. Padre Lane was the only stand where we found *Phalaris californica* Hook & Arn. and *Hierochloë occidentalis* Buckley and was one of only two stands with *Pinus radiata* (11%). Poppy Hills also had some *Pinus radiata* (2%), but was the only stand with *Rubus ursinus* Cham. & Schldl. or to have >1% *Arctostaphylos hookeri* G. Don (10%). Because these four stands have such exceptional composition, they confound analysis of the other open coastal prairies and were subsequently dropped from more detailed analysis of coastal terrace prairies.

Ordinations of species composition data from the 29 coastal terrace prairies showed that different land forms ("inland ridges," "coastal terraces," and "bald hills" above coastal terraces) each have a relatively distinct species composition. This was supported by results of the analysis of variance for individual measures. Comparisons of the three land forms of coastal terrace prairies showed that bald hills have more species of grasses and sedges overall (Table 3-a), more native grasses and sedges (Table 3-b) and more native forbs at both scales of sampling (Table 3-c, d) and so more species of native plants overall (Table 3-e). The cover of the native plants show a similar pattern—Bald Hills has more cover of natives (Table 3-f), particularly more cover of native perennial forbs (Table 3-g). Inland

ridges, as will be seen in a pattern extending to inland *Nassella* prairies (below) show more dominance by annual exotic forbs (Table 3-h) and other exotics in general (Table 3-i) than the more diverse, bald hill coastal terrace prairie.

Both inland *Nassella* prairies and coastal terrace prairies show an increase in the number of native species with total species richness in 0.1 ha plots (Figure 6-a, b). The number of exotic species also increases with species richness in inland *Nassella* prairies but not in coastal terrace prairies (Figure 6-c, d). The relative cover of exotics decreases in both inland *Nassella* prairies and coastal terrace prairies with species richness (Fig. 6-e, f). One relative outlier (Fig. 6-f) is instructive. This stand, Piedras Blancas-1, is unusually low in both relative cover of exotics and species richness because it is the only stand with 95% cover of one native, the perennial grass (*Deschampsia cespitosa* var. *holciiformis*). In some cases then, relative cover of exotics can be low (~1%) even with low species richness (~34) if the total cover of the site is high. Including all coastal terrace prairies and inland *Nassella* prairies, species richness (0.1 ha) and total cover were positively correlated ($R^2_{\text{adj}} = 0.18$, $F = 24.8$, $P < 0.001$, residual $df = 107$) and relative cover of exotic species is negatively correlated with total cover ($R^2_{\text{adj}} = 0.19$, $F = 25.6$, $P < 0.001$, residual $df = 107$). Native species richness (0.1 ha) and exotic species richness were positively corre-

TABLE 3. BASED ON OPEN COASTAL GRASSLANDS, DIFFERENCES BETWEEN MEAN VALUES FROM COASTAL TERRACES (CT, N = 10), COASTAL BALD HILLS (BH, N = 10 AND INTERIOR DRY RIDGES (IR, N = 9) ARE SHOWN BASED ON ANALYSIS OF VARIANCE. Bonferroni/Dunn post-hoc comparison (e.g. BH, CT) are shown only with a significance level of 0.05. Residual df = 26 in all 2-way ANOVA. Arcsin-square root transformation of ratio data were done before ANOVA; results expressed below in ratios.

a. Species of Grasses and Sedges 0.1 ha			
	F = 3.61, mean	P = 0.04 std. error	
CT	14.5	1.2	
BH	15.4	1.4	BH, IR P ≤ 0.05
IR	11.0	0.8	
b. Species of Native Grasses and Sedges 2 sq. m			
	F = 6.1, mean	P = 0.006 std. error	
CT	14.5	1.2	
BH	15.4	1.4	BH, IR P ≤ 0.05
IR	11.0	0.8	
c. Species of Native Forbs 0.1 ha			
	F = 3.92, mean	P = 0.032 std. error	
CT	17.6	2.6	
BH	28.9	3.4	BH, CT P ≤ 0.05
IR	20.4	3.0	
d. Species of Native Forbs 2 sq. m			
	F = 3.45 mean	P = 0.04 std. error	
CT	9.7	1.9	
BH	17.1	2.3	BH, CT P ≤ 0.05
IR	13.4	1.9	
e. Species of Native Plants 0.1 ha			
	F = 4.39 mean	P = 0.02 std. error	
CT	25.1	2.9	
BH	36.7	3.8	BH, IR P ≤ 0.05
IR	24.6	2.9	
f. Cover—Native Plants			
	F = 7.02, mean	P = 0.036 std. error	
CT	67.7	8.8	CT, IR P ≤ 0.01
BH	77.7	5.3	BH, IR P < 0.01
IR	42.9	4.6	
g. Cover—Native Perennial Forbs			
	F = 3.89, mean	P = 0.035 std. error	
CT	12.2	2.7	
BH	21.4	4.7	BH, IR P ≤ 0.05
IR	8.6	1.6	
h. Cover—Annual Exotic Forbs			
	F = 6.84, mean	P = 0.004 std. error	
CT	9.7	2.3	CT, IR P ≤ 0.05
BH	6.9	1.7	BH, IR P ≤ 0.05
IR	20.6	3.9	
i. Ratio of Exotic Species/Total Forb Cover			
	F = 4.86, mean	P = 0.016 std. error	
CT	0.48	0.069	
BH	0.37	0.048	BH, IR P < 0.05
IR	0.63	0.025	

lated for inland *Nassella* prairies ($R^2_{adj} = 0.23$, $F = 24.6$, $P < 0.001$, residual $df = 78$) but not for coastal terrace prairies ($R^2 = 0.02$, $F = 0.67$, $P < 0.001$, residual $df = 27$).

Considering just the 29 open coastal terrace prairies, grasses and forbs differ in how they vary with species richness at 0.1 ha. On this scale, neither total vegetative cover nor cover of native species is related to species richness. However, cover of all exotic species decreases significantly with increasing species richness ($R^2_{adj} = 0.15$, $F = 6.0$, $P < 0.05$, residual $df = 27$). This decrease in cover of exotics with an increase in species richness was largely due to the decrease in cover of exotic grasses. Cover of exotic grass was significantly negatively correlated with species richness ($R^2_{adj} = 0.12$, $F = 4.96$, $P < 0.05$, residual $df = 27$). Neither the cover of exotic forbs or the number of exotic forbs was correlated with species richness in coastal terrace prairies. The degree to which the grasses are native increases with species richness; the number of native grasses is correlated with species richness ($R^2_{adj} = 0.14$, $F = 5.56$, $P < 0.05$, residual $df = 27$) although the cover of native grass is not correlated. The degree to which forbs are native also increases with increasing species richness. In this case both cover and number of native forbs (0.1 ha) were significantly correlated with species richness (respectively, $R^2_{adj} = 0.29$, $F = 12.9$, $P < 0.001$, residual $df = 27$ and $R^2_{adj} = 0.83$, $F = 136$, $P < 0.001$, residual $df = 27$).

The summary of the 25 most frequent and dominant species of grasses and sedges in the coastal prairies (Fig. 4) reveals that coastal prairies are heavily invaded with non-natives. The widespread fescue, *Vulpia* spp. is in most samples and is often very abundant. *Danthonia californica*, *Nassella pulchra*, and *Festuca rubra* are the native grasses that define this community. A summary of the 25 most frequent and dominant species of forbs in coastal prairies (Fig. 5) show a similar dominance by non-natives; in this case by widespread *Plantago*, *Erodium*, and *Hypochaeris*, all of which extend well inland. Most important natives include the very similar *Plantago erecta* E. Morris and *Baccharis pilularis*. These natives, along with *Viola*, *Sidalcea*, *Cannisonia*, and *Acaena* are the native forbs that complete the definition of these coastal prairies. In this community, the dominance of grasses drops off rapidly (Fig. 4), while the cover and frequency of the forbs is far greater for more species (Fig. 5).

Dominance of exotic grasses and forbs in coastal terrace prairie increases inland coastal terraces, to bald hills, and further to the drier ridges (Table 3). For coastal prairies, the average ratio of the number of exotic grass or sedge species to total species present is 0.44, and the average ratio of exotic forb species is 0.33 ($n = 33$). Corresponding average ratios of exotic species in inland *Nassella* prairies are 0.79 and 0.19 ($n = 80$).

TABLE 4. STAND NAMES AND LOCATIONS (UTM) INCLUDED IN SAMPLING OF CALIFORNIA COASTAL GRASSLANDS.

No.	Stand name	Abbreviation	East	North	Soil type
1.	Barker Ranch, Laureles Ridge	Barker 1	614.291	4041.710	Sandy Loam
2.	Barker Ranch, Laureles Ridge	Barker 2	613.835	4041.865	Sandy Loam
3.	Bird Rock, Inland terrace	Bird Rock 1	593.202	4050.157	Sand
4.	Bird Rock, Inland terrace	Bird Rock 2	593.177	4050.126	Sand
5.	Canada Woods Site No. 4	CW No. 4	603.776	4051.868	Clay Loam
6.	Canada Woods, Garage Site	CW Garage	604.100	4047.500	Clay Loam
7.	Canada Woods, Lower Pine Tree	CW Low Pine	603.500	4048.200	Clay Loam
8.	Canada Woods, Pine Tree	CW Pine Tree	606.660	4049.100	Clay Loam
9.	Canada Woods, Swale	CW Swale	603.800	4046.900	Clay Loam
10.	Canada Woods, Big Pool	CW Big Pool	604.085	4046.295	Clay Loam
11.	Fish Ranch, above Entrance Rd.	Fish Ranch 1	597.300	4042.694	Silty Loam
12.	Fish Ranch, above Entrance Rd.	Fish Ranch 2	597.313	4042.692	Silt Loam
13.	Fort Ord, opposite Toro Park	Ft. Ord Toro	615.941	4052.110	Sandy Loam
14.	Jade Flat, Central Terrace	Jade Flat	638.283	3975.370	Serpentine Clay
15.	Laureles Grade, Laureles Ridge	Laureles	611.870	4043.319	Sandy Loam
16.	Molera State Park, N. Terrace	Molera	602.546	4016.610	Sand Loam
17.	Olson Hill, Diablo Canyon	Olson Hill	698.859	3896.149	Loam
18.	Pebble Beach, 24 Padre Lane	Pebble For	592.366	4048.055	Loamy Sand
19.	Plaskett Ridge, Above Camp	Plaskett Rdg	638.277	3975.359	Serpentine Rock
20.	Point Lobos, Escobar Flat	Pt. Lobos Flat	597.250	4042.194	Sandy Loam
21.	Point Lobos, Mima Mounds	Pt. Lobos Mima	584.700	4041.300	Clay Loam
22.	Poppy Hills, Opposite Golf Club	Poppy Hills	595.225	4048.980	Sandy Loam
23.	Pt. Piedras Blancas Light House	Piedras LH	646.262	3948.422	Sand
24.	Pt. Piedras Blancas Terrace 1	Piedras 1	654.425	3951.349	Loam
25.	Pt. Piedras Blancas Terrace 2	Piedras 2	654.347	3951.341	Loam
26.	Rancho San Carlos, Animas Entr.	Danthonia RSC	600.086	4040.213	Clay Loam
27.	Rancho San Carlos, Animas Rdg.	Animas RSC	600.071	4041.197	Clay Loam
28.	San Bruno Mtn., Great Meadow	San Bruno 1	548.059	4171.974	Loamy Sand
29.	San Bruno Mtn., Great Meadow	San Bruno 2	549.274	4171.733	Loamy Sand
30.	San Louis Hill, Diablo Canyon	San Luis Hill	703.599	3893.915	Clay Loam
31.	Soda Springs, Bluff W. of Hwy 1	Soda Spring	646.266	3965.330	Serpentine Rock
32.	Spruance Meadow, Spruance Dr.	Spruance	595.662	4047.953	Loamy Sand
33.	Work Ranch, Hwy 68	Work Ranch	603.586	4048.821	Sandy Loam

We used CCA to sort out which individual comparisons of community characteristics (measures of diversity and the degree of invasion by exotic species) are most closely associated with vegetation composition across the landscape gradient from inland *Nassella* prairies to coastal terrace prairies. Some of these measures were highly correlated, so we proceeded with only 19 (Table 5). Plant species with total cover of less than 0.05% and which occurred in 5 or fewer stands were eliminated, leaving 192 species. With these simplifications (tolerance set to 0.100000E-12), PCord reached a CCA solution after fewer than 100 iterations. Inland *Nassella* prairies were clearly grouped to the left (Fig. 7) and coastal terrace prairies were on the right. The highest "intra-set correlation" (ter Braak and Smilauer 1998) with this first axis was the cover of native, perennial grass and on the second axis, the cover of exotic species (Fig. 7). Coastal terrace prairies are characterized as having both more species and higher cover of native perennial grasses than any of the tightly grouped (thus similar) inland *Nassella* prairies that are clearly placed to the left of the first axis where stands can be described as having higher cover of annual, exotic forbs (for example, *Erodium cicutarium* (L.) L. Hér.). The second axis dis-

tinguishes between coastal terrace prairies into those with relatively more dominance by exotic species (Piedras Blancas Light House, Fish Ranch, etc.) and those with relatively high cover of native, perennial forbs (San Bruno, Soda Springs, Piedras Blancas 1, etc.) (Fig. 7—joint plot).

By restricting our focus to only coastal terrace prairies, we can examine the pattern of species composition and floristic characteristics at a smaller scale. By dropping the 80 inland *Nassella* prairies, the number of plant species (total cover >0.5%) included in the CCA dropped to 149. Correspondingly, more of the floristic variables were highly correlated (Table 5) and only 12 were relatively independent. A joint plot (Fig. 8) shows many coastal terrace prairies in a group with relatively high cover of exotic species. The highest intra-set correlation with the first axis was with cover of exotic species. The highest intra-set correlation with the second axis was with the number of native forbs. Stands such as San Bruno, Soda Springs, the stands near Avila Beach (Olson Hill, San Luis Hill) are exemplary coastal terrace prairies with fewer exotics and higher cover of native forbs. The Point Lobos Mima mound prairie and Piedras Blancas 1 are coastal terrace prairies with fewer exotics, higher

Dominant Grasses/Sedges - Coastal Grasslands

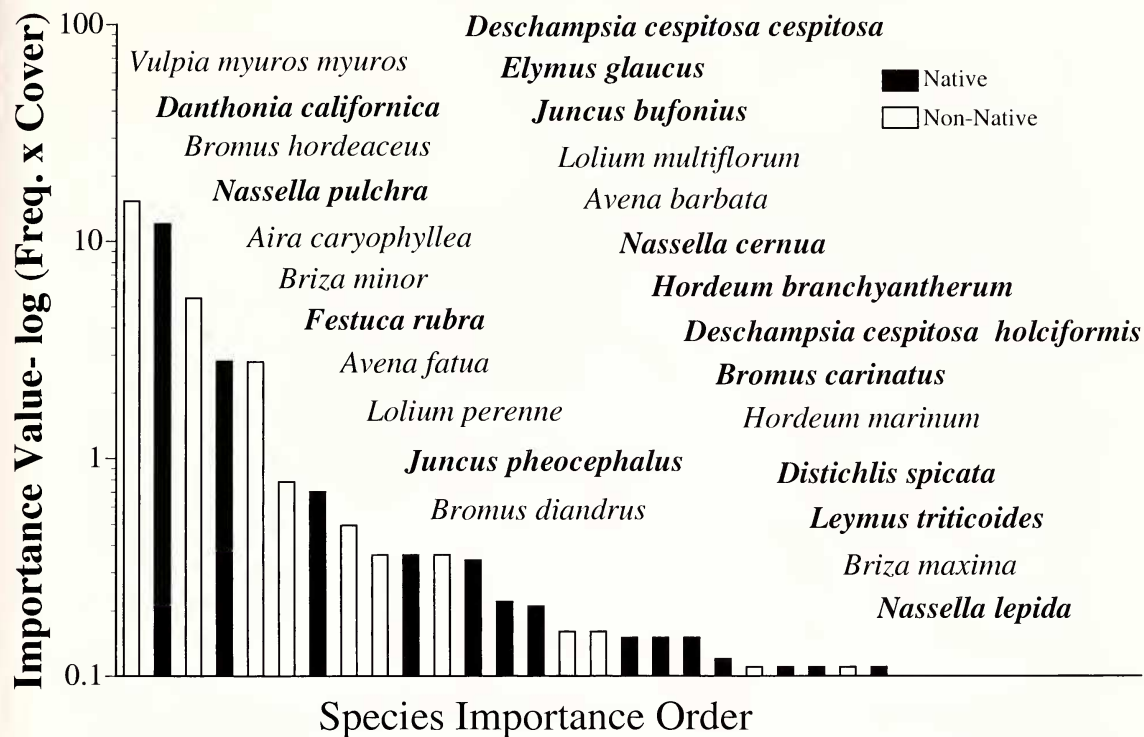


FIG. 4. Importance value (frequency \times average percent cover) of the 25 most dominant species of grasses and sedges, averaged from 29 coastal terrace prairies in central, coastal California.

cover of native forbs and more native grasses (Fig. 8—joint plot) while stands clustered on the left side relatively more cover of exotic species.

Soils and locations of the various sites are described in Table 4. Fourteen of the coastal terrace prairies (44%) occurred on soils with a hardpan from 10–20 cm beneath the surface. An additional three coastal terrace prairies occurred on serpentine rock or clay with limited drainage. A hardpan that provides standing water during the winters was often present, but apparently not required. Coastal terrace prairies also occurred on sands, loams and clays.

DISCUSSION

Diversity of plant species in coastal terrace prairies is among the highest in grasslands of North America (Stohlgren et al. 1999b). County and wildland planners often have selected coastal terrace prairies for development, perhaps not recognizing the biodiversity of coastal terrace prairies or because political support to protect forests or coastal scrub has been comparatively well organized. If protection of biodiversity is a goal, then coastal terrace prairies should be protected and development should be focused on relatively species-poor plant communities.

Invasions of natural communities by exotic spe-

cies may occur more readily in areas of low species diversity than in areas of high species diversity (Darwin 1859). Plant communities with low species diversity (and total cover) may use resources less completely, allowing invasion by similar species (MacArthur and Wilson 1967; Pimm 1991; Tilman et al. 1997). Evidence for this relationship between diversity and invasions in grasslands depends on scale, and at a landscape scale, may be reversed (Stohlgren et al. 1999b). Based on the number of species, our studies do not support the theory that exotics are more abundant where species diversity is relatively low; inland *Nassella* prairies (but not coastal terrace prairies) with the highest diversity have more exotic species (Fig. 6c, d). But, numbers of species probably do not reflect ecosystem function. Species occupying more space intercept more light, and presumably are more important in nutrient capture and storage. In both inland *Nassella* prairies and coastal terrace prairies, most species in our grasslands have cover $<5\%$. Two species may be equally counted as present, but one may occupy far more cover in the community. Based on relative cover (Figs. 6e, f, 7) both diverse inland *Nassella* prairies and coastal terrace prairies have reduced exotic dominance, supporting the theory that less diverse communities are more likely to be invaded.

Ordinations of the species and stands agree with

Dominant Forbs - Coastal Grasslands

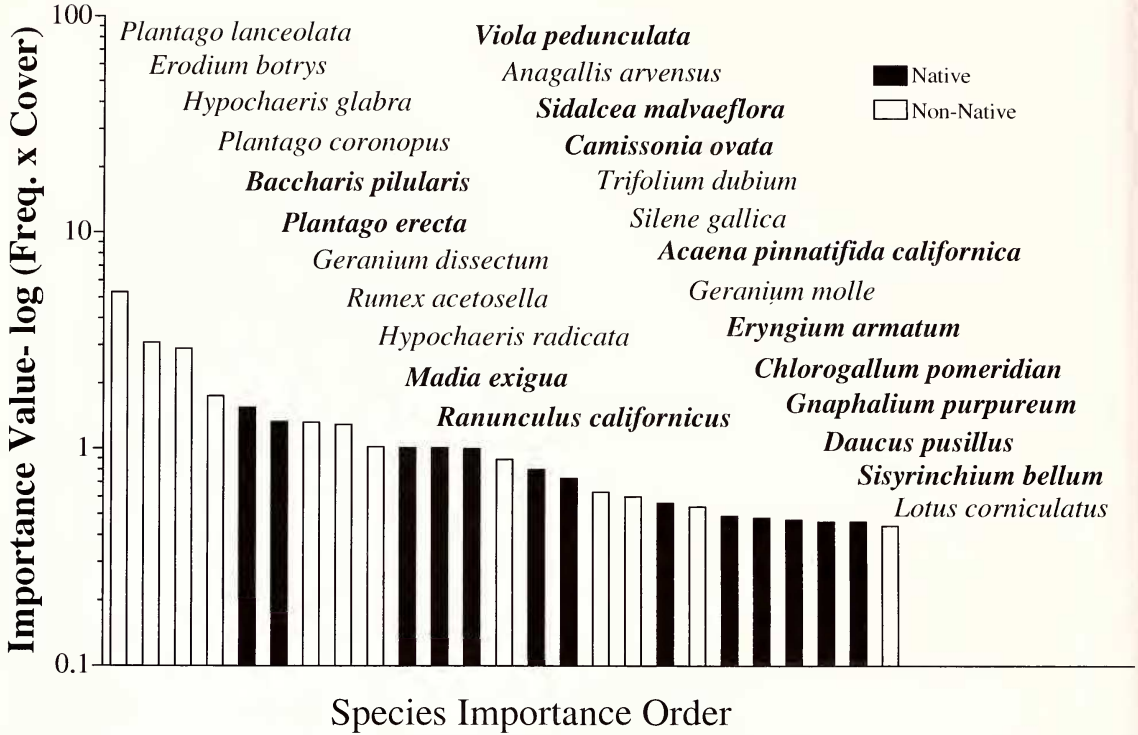


FIG. 5. Importance value (frequency × average percent cover) of the 25 most dominant species of forbs, averaged from 29 coastal terrace prairies in central, coastal California.

our general understanding of the biology of individual species. The ordinations are also consistent with patterns seen by making pairwise statistical comparisons (Table 3, Fig. 7). All coastal terrace prairies have been invaded to some degree by exotics, but the importance of exotic species is far greater in inland *Nassella* prairies. Two of the three grasses with the most cover (Fig. 4) and the four forbs with the most cover in coastal terrace prairies are exotics (Fig. 5).

Although the effects of grazing by large domestic herbivores on these grasslands were not specifically addressed, a re-analysis of inland *Nassella* prairie data at various scales of sampling (Figs. 2, 3) supports observations elsewhere that the loss in plant species diversity in grasslands grazed by herbivores is only seen at a scale larger than about 100 m² (Chaneton and Facelli 1991, Olf and Ritchie 1998). Grazing, or its removal, probably has little effect on species diversity in other California grasslands because grazing has been continuous for centuries following European settlement (Harrison 1999). At some scales, grazing may have little effect on native species richness in other North American grasslands (Stohlgren et al. 1999a). All grasslands in this study were probably grazed since European settlement. There is no evidence that

herds of large herbivores co-evolved with the California coastal grasslands (Painter 1995). In general, domestic livestock grazing has had severe impacts on grassland ecosystems in western North America (Painter and Belsky 1993) and livestock removal has been suggested at various scales (Bock et al. 1993). However, grazing has been present for so long that careful consideration must be given before livestock are removed from coastal grasslands. On Santa Cruz Island, grasslands formerly grazed by cattle now support near monocultures of *Foeniculum vulgare* Miller, an exotic plant formerly held in check by year-long grazing (M. Stromberg pers. obs., Mayfield et al. 2000). On other coastal parklands where grazing has been entirely removed after many years of year-round grazing (Andrew Molera State Park, Santa Clara County Parks, San Mateo County's Mid-Peninsula Open Space District) we have seen extensive, rapid expansions of *F. vulgare*, *B. pilularis*, and *Dipsacus* spp. where these plants were formerly relatively unimportant.

Most coastal terrace prairies were clearly open grasslands, but the composition of several stands included trees and shrubs (e.g., Poppy Hills, Padre Lane). The presence of otherwise typical coastal terrace prairies grasses and forbs in these brushy or

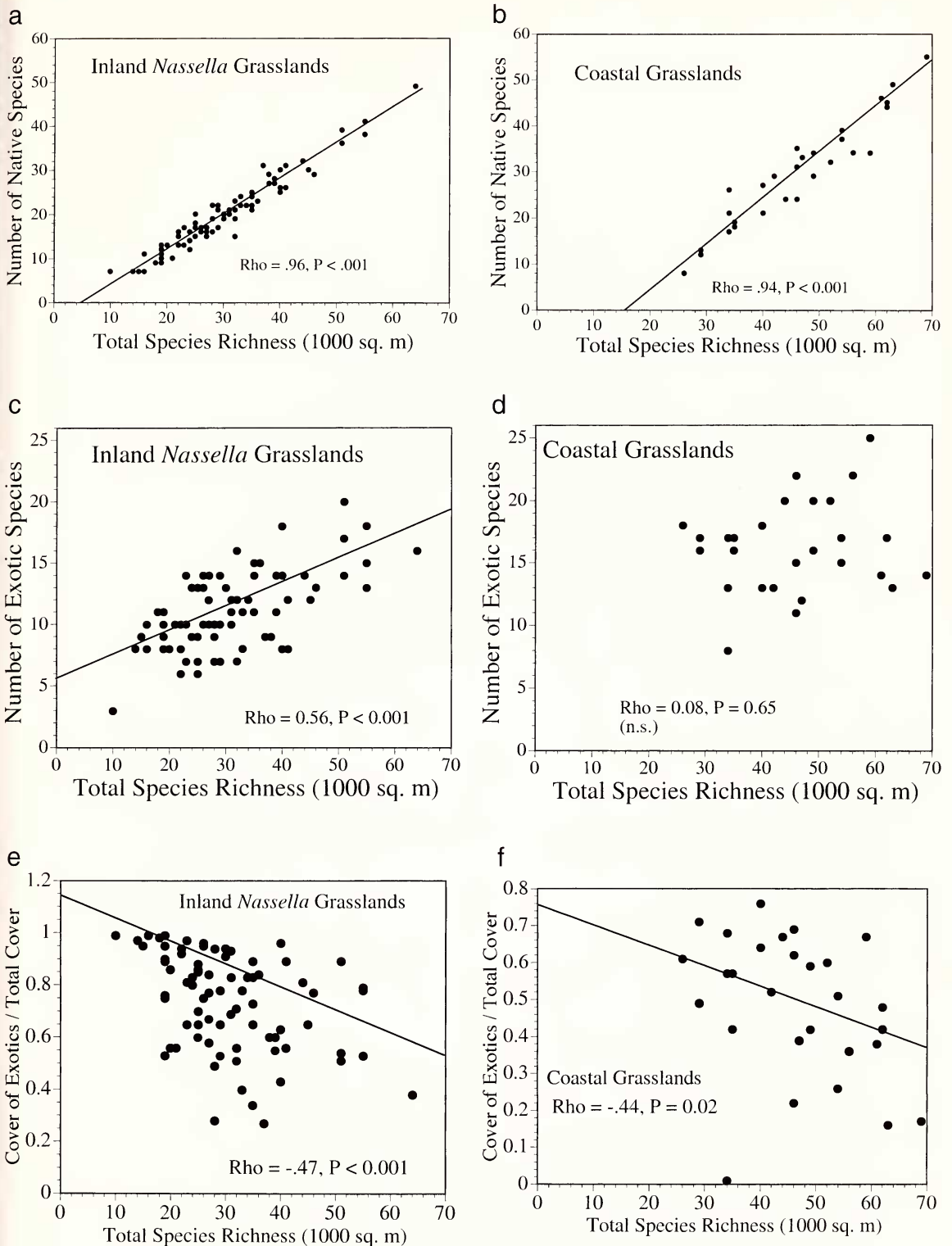


FIG. 6. Spearman rank correlation between species richness and number of all native plant species for a.) 80 inland *Nassella* prairies and b.) 29 coastal terrace prairies. Spearman rank correlation between species richness and number of all exotic plant species for c.) 80 inland *Nassella* prairies and d.) 29 coastal terrace prairies. e. Spearman rank correlation between species richness and relative cover of exotic plant species for e.) 80 inland *Nassella* prairies and f.) 29 coastal terrace prairies.

TABLE 5. FLORISTIC VARIABLES CONSIDERED IN ANALYSIS OF SPECIES RICHNESS IN CALIFORNIA GRASSLANDS. Highly correlated variables were dropped, leaving 19 variables (middle column) with sufficiently minimal correlation required to compute canonical correlation analysis (Fig. 6). When only 29 coastal terrace prairies are compared, 12 floristic variables were included in the analysis (Fig. 7). For example, in a CCA including 80 INP and 29 CTP, variable 1 (No. of Species in 2 sq. m) was dropped as it had a high correlation with variable 21 (No. of all Natives).

No.	Variable name	Correlated variable(s) no., R ²	
		80 INP and 29 CTP	29 CTP
1.	No. of Species in 2 sq. m	21, .94	21, .92
2.	No. of Species in 0.1 ha	25, .87	25, .91; 27, .95
3.	Total Vegetative Cover	included	included
4.	Cover of all Exotics	included	included
5.	Cover of all Natives	8, .78; 17, .79; 6, .86	6, .80
6.	Cover of Native, Perennial Grass	included	included
7.	Cover of Native, Perennial Forbs	included	included
8.	No. of Native, Perennial Grasses (0.1 ha)	17, .92; 23, .99	23, .99
9.	No. of Native, Perennial Forbs (0.1 ha)	included	25, .91
10.	Cover of all Exotic Grasses (0.1 ha)	included	4, .91
11.	Cover of all Exotic Forbs (0.1 ha)	included	included
12.	Cover of Annual, Exotic Grasses	4, .99	4, .90
13.	No. of Annual, Exotic Grasses (0.1 ha)	included	16, .84; 22, .94
14.	Cover of Annual, Exotic Forbs	included	included
15.	No. of Annual, Exotic Forbs (0.1 ha)	included	24, .92
16.	No. of Exotic Grasses (2 sq. m)	included	22, .88
17.	No. of Native Grasses (2 sq. m)	8, .94	8, .82; 23, .87
18.	No. of Exotic Forbs (2 sq. m)	included	20, .86
19.	No. of Native Forbs (2 sq. m)	included	included
20.	No. of all Exotics (2 sq. m)	included	included
21.	No. of all Natives (2 sq. m)	included	included
22.	No. of all Exotic Grasses (0.1 ha)	13, .96	13, .94
23.	No. of all Native Grasses (0.1 ha)	included	included
24.	No. of all Exotic Forbs (0.1 ha)	included	26, .86
25.	No. of all Native Forbs (0.1 ha)	included	included
26.	No. of all Exotics (0.1 ha)	included	included
27.	No. of all Natives (0.1 ha)	25, .94	25, .95

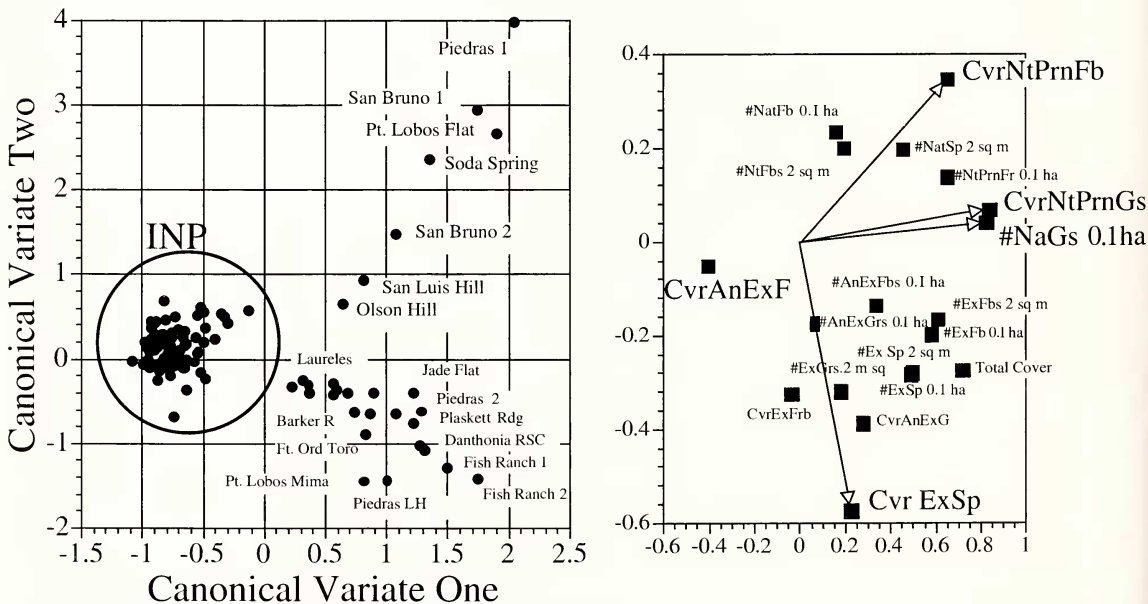


FIG. 7. Canonical correspondence analysis (ter Braak 1994) of 80 inland *Nassella* prairies and 29 coastal terrace prairies, based on cover of 197 plant species and 19 floristic variables. Inset: joint plot of stands and correlated floristic variables for all stands; length of vector associated with each variable is related to correlation with position of stand on canonical axes; highly correlated floristic variables are plotted near each other.

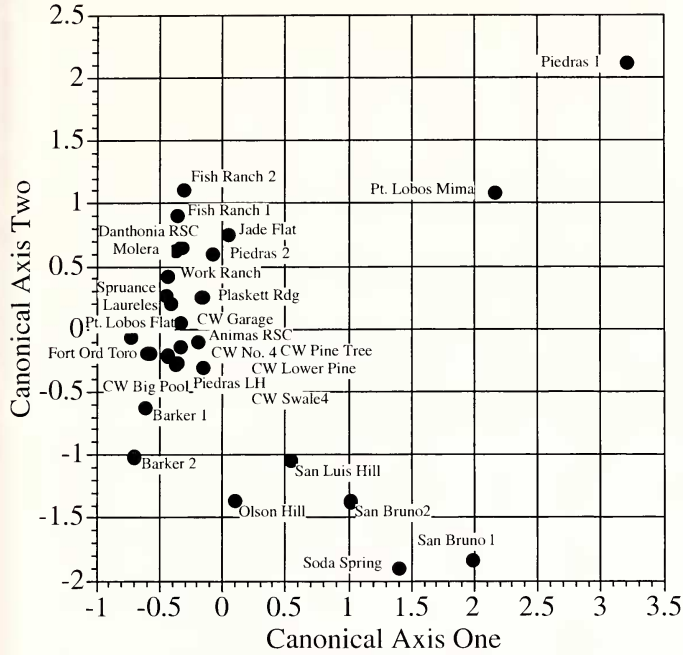


FIG. 8. Canonical correspondence analysis of 29 coastal terrace prairies based on cover of 149 plant species and 12 floristic variables. Inset: joint plot of floristic variables for axes one and two.

forested stands supports the concept of a dynamic tension between forest and grassland vegetation mediated by occasional fire (or grazing) in the coastal communities (Greenlee and Langenheim 1990). Currently, central California coastal grasslands are gradually seeing increased dominance by the native coastal shrub (*B. pilularis*) (McBride and Heady 1968) or oak woodland (Callaway and Davis 1993). Indeed, *B. pilularis* is a co-dominant native of the coastal prairies.

California's human population will double by 2040, and coastal development is much faster than that in interior California (Medvitz and Sokolov 1995). Although prescribed fires are the most cost-effective way to maintain the grasslands on a large scale (Kephart 2000), current and planned development almost precludes this option. Small-scale prescribed burns, mowing, and controlled grazing during the dry season should be included in management strategies to sustain the long-term viability of California's coastal prairies.

Although some may attempt to assign names or define units of vegetation (Sawyer and Keeler-Wolf 1995) this may be impossible (Zedler 1997) because vegetation occurs on a continuum in the environment where each species has an individual distribution on the gradient from coastal to inland. Even if we could find identical environments, species composition would probably vary due to other factors that have undoubtedly influenced the abundance of individual species in a given year (Fox and Fox 1986). Gradients may also be based on

competition; from wet (coastal) to dry (inland) (Lane et al. 2000) or disturbance (fire frequency, grazing duration and intensity, gopher abundance, etc.).

Gopher tailings probably sustain a disturbance regime of inland California annual grasslands and old fields (Stromberg and Griffin 1996) where gopher density can be very high. On coastal terrace prairies, however, gopher tailings rarely observed.

We did not sample all known high-quality or relict stands in this study area. Terraces on the San Simeon Ranch, the grasslands just north of Santa Cruz adjacent to Wilder Ranch State Park, those on the San Mateo coast, and those north of Bodega Bay need more investigation.

Coastal prairies support a number of state or federally designated "rare" species and are often managed for protection of rare animals (Launer and Murphy 1994). Rare animals include several butterflies; the Mission Blue and San Bruno Elf (McClintock et al. 1990, Weiss 1993). Conservation of the coastal terrace prairie on San Bruno Mountain includes the first "habitat conservation plan" approved by the federal government. Species considered as "special plants" by various regulatory agencies and observed in this study include: *Arctostaphylos hookeri* G. Don, *Astragalus tener* A. Gray var. *titi* (Eastw.) Barneby, *Allium hickmanii* Eastw. (in 23% of the coastal terraces sampled), *Sanicula maritima* S. Watson, *Trifolium polyodon* E. Greene, *Psilocarphus tenellus* Nutt. var. *globiferus* (DC.) Morefield, *Cirsium occidentale* (Nutt.)

Jepson var. *compactum* Hoover, *Perideridia gairdneri* (Hook & Arn.) Mathias, and *Arabis blepharophylla* Hook & Arn. Each of these officially rare species occurred in only one stand, and then only sparsely in the larger plot (50 m × 20 m, 0.1 ha). We also found *Ophioglossum californicum* Prantl at Spruance Meadow, not seen in Monterey County since its original collection in 1910. *A. t.* var. *titi* is federally listed as endangered and occurs only in one location (Bird Rock). We purposely included this site in the sampling as it occurs on an exceptional relict stand including *Danthonia* and *Deschampsia cespitosa* var. *holciformus*. Land managers who can identify the species assemblages described here (Figs. 4, 5) should expect other associated rare species.

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